

LIFE-HISTORY OF BOCCARDIA HAMATA (WEBSTER) ON THE EAST AND WEST COASTS OF NORTH AMERICA

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Polydora hamata Webster, 1879, was recently transferred to the closely related genus *Boccardia*, and *Boccardia uncata* Berkeley, 1927 and *Polydora uncatiformis* Monro, 1938 were placed in synonymy with *B. hamata* (Webster), a new combination (Blake, 1966). This species has been reported from a variety of muddy estuarine habitats on the west coast as *B. uncata* (Hartman, 1961) and as *B. hamata* (Blake, 1966). From Japan, Okuda (1937) collected *Polydora* (*Boccardia*) *uncata* “. . . from a muddy flat between crevices of rock.” On the east coast of North America (Webster, 1879) and the Gulf of Mexico (Hartman, 1951; Rioja, 1960) this species has been recorded as *P. hamata* and has been found only in galleries of shells. Re-examination of the specimens identified as *Polydora* sp. (Dean and Haskin, 1964, tables 5 and 6) has shown them to be *B. hamata*. The specimens inhabited tubes of fine sediment on rocks between bases of the barnacle, *Balanus improvisus*.

In these two independent studies development was followed from eggs to young adults on the east coast and from the earliest planktonic larvae to young adults on the west coast. These two studies were synthesized and larval development from both coasts compared in the present paper.

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MATERIALS AND METHODS

1. East coast study

Adults of *B. hamata* were found inhabiting burrows in shells of the hermit crab, *Eupagurus pollicaris* and in bottom samples of fine sand-shell mixture at 5 to 6 m. in one locality of the Mystic River. Adults for this study were obtained by cracking open hermit crab shells and examining the shell fragments with a dissecting

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microscope. A male containing motile sperm was obtained on April 2, 1963. On July 10, 1963, a partially exposed egg string was found in a burrow with an adult female *B. hamata* in the shell of *Lunatia heros*. The piece of shell with the partially exposed egg string was washed in several changes of filtered sea water. One sac was dissected from the string and placed unruptured in a separate dish so that development could be observed. Two more of the exposed sacs were ruptured during the following week to release some of the larvae for study. The rest of the string was left intact. Once or twice daily the dishes were examined for released larvae. Groups of five or more larvae of the same stage of development were placed in rearing vessels and fed a suspension of liver-powder—once a week for young stages, up to three times a week for late stage larvae. Rearing techniques have been described previously (Dean and Hatfield, 1963a; Dean, 1965; Hatfield, 1965). Specimens from the above source were maintained in laboratory culture until October 2, 1963.

Larvae were examined periodically under phase optics using either hanging drop or Saran Wrap techniques (Dean and Hatfield, 1963b). The accompanying Figures 1-5 are composite drawings made from photographs, sketches and descriptions.

Once the larval development of *B. hamata* was known, additional larvae were obtained from plankton samples for studies on metamorphosis and larval behavior. Plankton tows, taken at approximately weekly intervals throughout the year, have yielded larvae of this species from late June to late September. They have been most abundant, however, in August.

2. West coast study

Plankton samples were taken in Morro Bay at monthly or more frequent intervals from May 16 to September 3, 1964. *Boccardia hamata* larvae were encountered in all samples but were most abundant during June and July. Living material was brought to Fresno (a distance of 175 miles from the coast) in an insulated ice chest. In an air conditioned laboratory the larvae were sorted as soon as possible and placed with sea water in 60-mm. or 90-mm. diameter plastic Petri dishes or in battery jars with an aerator. Larvae survived better in the dishes. The larger dishes contained three compartments and were used for comparative studies of the influence of various substrata on settling and metamorphosis. A different type of substratum was put in each compartment and enough sea water added to allow larvae equal access to all substrata. The larvae were fed cultures of *Dunaliella*, dried and pulverized macroscopic alga, *Tethys* eggs or dead copepods from plankton samples.

Larvae were observed with a phase-contrast microscope. Most were placed on slides and covered with either Saran Wrap (Dean and Hatfield, 1963b) or coverslips. Some were observed in depression slides to allow greater freedom of movement. Photographs were taken with Polaroid and 35 mm. camera attachments. Figures 6 and 7 were prepared from photographs, sketches and notes.

Boccardia hamata adults were obtained from the silty mud of Morro Bay during Dec., 1963; Sept. and Dec., 1964; and Jan. and Feb., 1965. Neither ovigerous females nor egg capsules were collected; however, a male obtained in January of 1965 contained sperm.

RESULTS

1. *Development of east coast larvae*

Larval development of *B. hamata* on both coasts was found to be alike in almost all details. A few significant differences have been discovered and are discussed in the next section.

The moniliform egg string within the *Boccardia* burrow was similar to that figured for *Polydora ciliata* and *Polydora hoplura* (Wilson, 1928). Each sac in the exposed portion of the string contained 10 to 12 moving embryos. The number of sacs hidden within the burrow was not determined.

Trochophores were released from the ruptured sac on July 10. At this stage the prototroch completely encircled the anterior end and a large area on the ventral surface was ciliated. By the following day one pair of black eyes and a telotroch had developed (Fig. 1). An apical tuft was not observed at any stage. By July 13th larvae in the sacs had developed to a 3-setiger stage with melanophores, prototroch, telotroch and two pairs of eyes. All segments had long capillary serrate

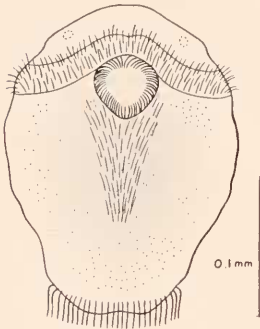


FIGURE 1. Trochophore in ventral view.

swimming setae, those of the first being slightly longer. Although gastrotrochs, neurotrochs and nototrochs were not observed, the larvae were capable swimmers when removed from the sac. By July 15th the larvae had developed to a stage with four setigerous segments and one non-setigerous segment (Fig. 2). A nototroch was present on setiger 3 and a neurotroch extended posteriorly from the mouth through setiger 1.

On July 18th almost all larvae emerged from the remaining sacs to begin their pelagic life. At this time the larvae had six setigerous segments and one non-setigerous segment anterior to the pygidium. These larvae were similar to the stage shown in Figure 2 except for size, the presence of gastrotrochs on setigers 3 and 5 and additional nototrochs on setigers 4 and 5.

The most obvious characteristics that serve to identify all pelagic stages of this species are the pigment patterns and general shape. Details of these and other morphological features are given below.

Pigment distribution is arranged in a definite pattern except for minor variations between individuals. Dorsally all segments have one pair of lateral stellate melanophores. A lateral process of the melanophores forms a small patch of pigment at the base of nearly all notopodia. Often setigers 1 and 5 lack these patches. All

but setiger 2 have additional dorsal pigmentation. On setiger 1 a heavy transverse band of black pigment extends across the anterior edge of the segment and coalesces with the lateral stellate chromatophores (Figs. 3 and 4). This concentration of pigment causes setiger 1 to appear darkest, when viewed dorsally, on all larvae up to the 19-setiger stage. On the anterior edge of setiger 3 there is a transverse band of pigment composed of two melanophores that have usually coalesced medially. Near the posterior edge of this setiger are two smaller melanophores on either side of the midline. From setiger 4 posteriorly, paired patches of pigment are found near the midline and near the posterior edge of each segment. The latter pigment patches appear, under high magnification, to be composed of

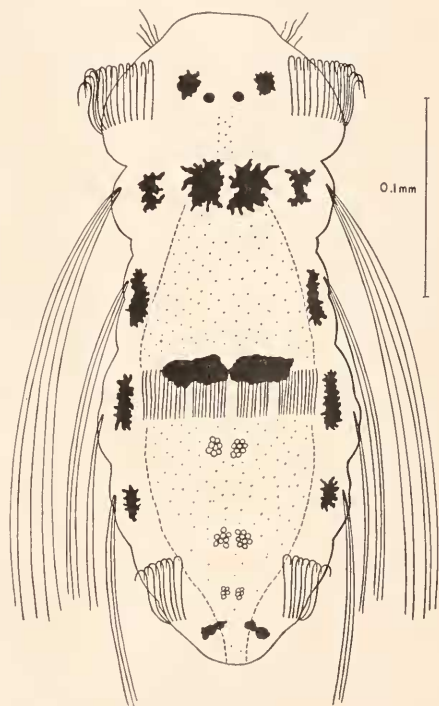


FIGURE 2. Four-setiger pre-pelagic larva in dorsal view.

hollow black spheres (Fig. 2). Collectively, the spheres give a black coloration (Figs. 3, 4, and 5). Two concentrations of black pigment appear dorsally on the pygidium. The pygidium has a granular brown hue which is broken by a transverse clear band caused by the unpigmented telotroch cells. The anterior ring of the prostomium is usually dusky brown and deepens in hue medially in swimming-crawling stages.

The most obvious ventral pigmentation is a longitudinal bar of black pigment on each lateral lip. These bars are so dense and large that their location can be seen through the larvae in dorsal view (Fig. 3) and in lateral view (Fig. 4). The remaining ventral pigmentation is usually located on the extreme posterior edges of the segments beginning with the third setiger (Fig. 4). On some specimens

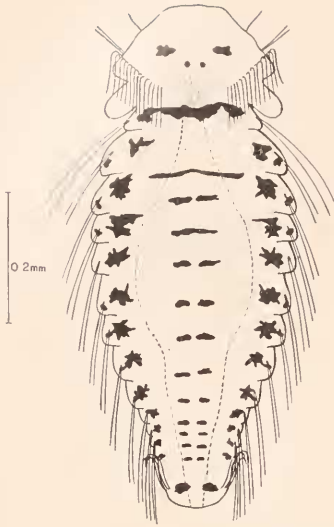


FIGURE 3. A pelagic 12-setiger larva in dorsal view. The thirteenth segment has been formed but its setae have not been secreted. Nototrochs and neurosetae have been omitted.

pigmentation also occurs on the anterior border of about setigers 4-7. Although the density of pigmentation here is highly variable between specimens, the pigment is usually arranged in two thin transverse stellate melanophores.

All pelagic stages are more or less fusiform in outline, regardless of whether they are viewed dorsally, ventrally or laterally.

Two pairs of eyes are almost always found on the larvae and are arranged as shown in Figures 2 to 5. On occasion, the larger and more anterior pair of eyes is divided giving the overall appearance of 3 pairs. At about the 13-setiger stage a cephalic crest or caruncle is formed (Fig. 4). By the 17-setiger stage the crest reaches the posterior edge of setiger 1 and the medial pair of eyes is high up on the crest.

Palps are first recognized in the 6- to 8-setiger larva as buds just anterior to the bases of the swimming setae of setiger 1. In the 13-setiger larva they are well developed and extend ventrolaterally to about the third segment (Fig. 4). In the

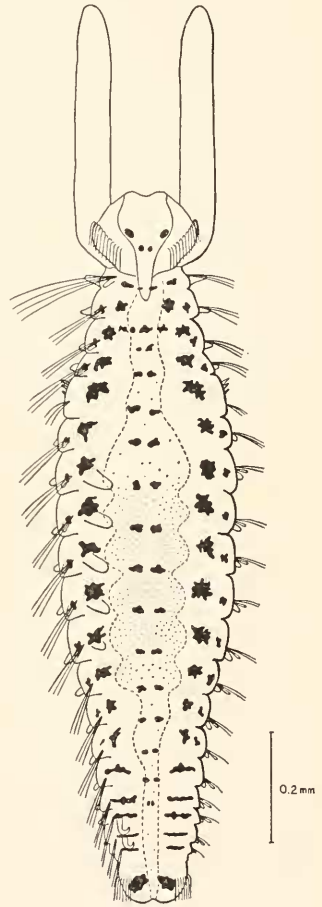


FIGURE 4. Thirteen-setiger pelagic larva in lateral view.

swimming-crawling stages the palps are extended while crawling (Fig. 5) or are tucked ventrally under the body while swimming.

The prototroch consists of a single row of stout cilia that passes laterally around the head of the larva from a point just anterior to the bases of the swimming setae of setiger 1 to the lateral lips. At the lips the prototrochal cilia grade into the shorter cilia that cover the oral region. The prototroch persists through the swimming-crawling stages and has been observed on some worms even after the larva

FIGURE 5. Nineteen-setiger swimming-crawling larva in the crawling position. Dorsal view. Neurosetae have been omitted on the left side. Notosetae and branchiae have been omitted on the right side.



has built a tube from sand grains. The telotroch consists of five indistinctly separated patches of cilia: one patch midventrally, two ventrolaterally and two dorso-laterally (Figs. 3 and 4). Gastrotrochs occur on setigers 3, 5, 7, 10, 13 and 15. The first gastrotroch is least developed. The remainder have longer cilia and extend across the ventral surface to the ventrolateral aspects of the body. Loss of gastrotrochs begins anteriorly with the disappearance of the first by the 13-setiger stage and the second by the 14-setiger stage.

Nototrochs, composed of four patches of cilia, make their first appearance on the third setigerous segment in the 4-setiger stage (Fig. 2). As a larva develops, prominent nototrochs appear on all setigers from 3 through 15. On late swimming-crawling stages much shorter cilia may also be observed on setigers 1, 2, 16, 17 and 18. Those on 1 and 2 are probably the beginning of nuchal ciliation while those on the posterior segments are probably the start of post-larval dorsal ciliation.

A poorly developed neurotroch extends posteriorly from the mouth through setiger 2. No ciliated pit was observed.

Sensory cilia are found on the anterior aspect of the prostomium.

All setae are capillary and serrate on larvae emerging from the egg sacs. The bases of the noto- and neurosetae are so close together that the larvae appear uniramous. During pelagic life the larval swimming setae are gradually replaced by non-serrate capillary setae and the distinction between noto- and neurosetae becomes more discernible. Hooded, bidentate crotchets first appear in the neuropodia of setiger 7 and are accompanied by curved, capillary setae. At the 15- to 19-setiger stage the slightly curved tips of the modified setae of setiger 5 begin to protrude from the body wall. The capillary noto- and neurosetae of this setiger are not as well developed as on adjacent setigers (Fig. 5). At the 19- to 20-setiger stage, a stout hooked seta accompanies the capillary setae in each notopodium of the posterior region (Fig. 5). In the east coast study the most anterior setiger bearing notohooks varied from 17 to 21.

Branchiae arise as outgrowths of the dorsal wall medial to the notosetae. These buds are not apparent until about the 15- or 16-setiger stage. By the 18-setiger stage, branchiae are conspicuous on setigers 7 through 11; those on 7 to 9 are well developed. Branchiae on segments anterior to the modified fifth setiger (a characteristic of the genus) do not appear in this species until sometime after the larvae have settled and metamorphosed into young adults.

At about the 19-setiger stage, the larvae begin a swimming-crawling phase. During this phase a larva will sink to the bottom of the vessel, lengthen and crawl over the bottom with a serpentine motion, then contract to the typical fusiform shape of the pelagic larva and resume swimming. At this stage the dense dorsal pigment of setiger 1 begins to break up and become rearranged as discussed later for the young adult.

Metamorphosis occurs at the end of the swimming-crawling phase when the larva loses its ability to resume swimming. In general, the amount of time spent on the bottom increases with increasing size. However, the stage at which individuals metamorphose varies greatly. The external morphological changes occurring at metamorphosis take several days to complete. Lengthening of the palps, loss of the telotroch and gradual reduction of the prototroch are the most apparent changes.

The rate of development of *B. hamata* larvae in the laboratory is shown in Table I. All observations were on specimens obtained from the egg string discovered on July 10, 1963. July 18, the day when the larvae were released naturally from the egg string, is taken as the beginning of pelagic life. The rate of development was relatively uniform between individuals for about the first three weeks of pelagic life. By the end of this time the majority of larvae had attained the 19-setiger stage. After the three-week period, the rate of development became more

TABLE I

Rate of development of Boccardia hamata larvae liberated from the same egg string

Date	Stage or setiger No.	Days after liberation
7-10-63	Trochophore	
7-11	Late trochophore	
7-13	3	
7-15	4	
7-18	6	0
7-19	6-7	1
7-23	8	5
7-24	9	6
7-29	13	11
7-31	12-16	13
8-5	19	18
8-6	17-19	19
8-11	15-20	24
8-12	23	25
8-14	18	27
8-23	23	36
8-24	22-30	37
9-18	19-27	62

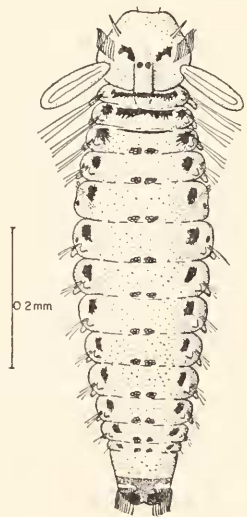
variable. Length of pelagic life of east coast forms is estimated to be two and one half to three weeks.

2. Development of west coast larvae

The foregoing account agrees with observations on west coast larvae except as noted below.

1) Differences in pigmentation: The dorsal pigment pattern includes a transverse band on the second setiger (Fig. 6). This band makes setigers 1, 2 and 3 appear

FIGURE 6. A pelagic 13-setiger larva from the Pacific coast in dorsal view. Nototrochs, gut and neurosetae have been omitted.



dark as opposed to only the first on east coast larvae. The pigment on the vestibule is never as strongly developed as on east coast forms. It is usually restricted to small black patches near the posterior borders of the vestibule. Ventral pigment on the body is often more strongly developed on west coast larvae and is usually restricted to setigers 3 to 7. Pigment is present in the intersegmental regions as shown in Figure 7.

2) Differences in ciliation: Gastrotrochs were not observed on setiger 3.

3) Differences in metamorphosis: Metamorphosis of west coast forms occurred very readily. Larvae usually metamorphosed between the 16- and 19-setiger stage, depending upon the substratum. In a few instances larvae with as few as 14

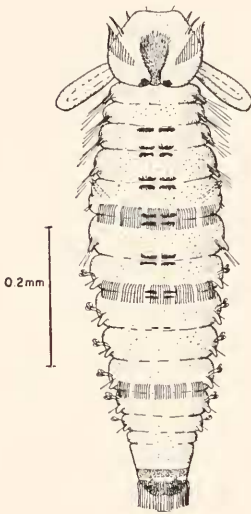


FIGURE 7. A pelagic 13-setiger larva from the Pacific coast in ventral view. Gut and notosetae have been omitted.

setigers metamorphosed. No larvae ever lived beyond 19 setigers without metamorphosing.

Mixtures of estuarine mud and open beach sand, ground coralline algae, and even planktonic detritus were used by the worms to construct tubes. Although larvae showed no preference for different substrata, growth after metamorphosis was fastest in those worms placed in estuarine mud. Following metamorphosis some specimens grew to over 40 setigers within three weeks.

During metamorphosis the segments lose their larval setae, leaving only those of the adult. The metamorphosed form is thinner and less fusiform than the pelagic larva. The head region and prostomium elongate and the latter becomes bilobate. The medial dorsal pigment bands on setigers 1 and 2 begin to shift forward and break up as the head narrows and elongates. The ventral pigment persists in its basic pattern through metamorphosis. Notosetae are lacking on setiger 1. A pair of fully developed modified setae with two bilimbate companion setae are present on each side of setiger 5. The pygidium elongates and small terminal processes possessing sensory cilia are evident for the first time.

3. *Post-larval development*

Post-larval development was best followed in west coast forms, due to their ease of metamorphosis and rapid growth. In specimens of 19 to 25 segments the anterior dorsal pigment pattern changes, forming an elongated mass of pigment on the caruncle posterior to the eye spots. Lateral to this a V-shaped pattern of pigment extends from the middle of segment 1 to the posterior margin of segment 2. This peculiar pattern begins to disappear at about the 34-setiger stage. The remaining dorsal pigment persists in its basic pattern only to about the 25-setiger stage, after which the inner rows of pigment become faint while the outer rows break up and disperse into small concentrated patches. On the 42-setiger worm, only an occasional patch remains, some near the notopodial lobes and others in the median region. This condition was also found in an adult specimen of 56 setigers taken from the shell of a hermit crab on June 28, 1961, from Cayucos, California.

The ventral pigment pattern persists, though faint, as late as the 42-segment stage.

Heavy, falcate hooks appear in the notopodia of posterior segments of either swimming-crawling stages or recently metamorphosed forms. As the worm grows, notohooks are formed in the newer segments and are lost in the older segments. For example, a 21-setiger specimen from the west coast had hooks on setigers 15 to 18, while on a 34-setiger specimen, hooks were present on setigers 26 to 32. Mature adults of 150 setigers have only 25 to 30 pairs of hooks in posterior segments.

The first branchiae to arise appear on setiger 7 as mentioned previously. As a worm grows, more branchiae are added posterior to setiger 7 and continue to the mid-region of the body. The appearance of branchiae on setigers 2, 3 and 6 does not occur until approximately three weeks after metamorphosis has been completed, regardless of the size of the specimen. For example, on the east coast, a 23-setiger worm that had metamorphosed three weeks previously had branchial buds on setigers 2, 3 and 6; a swimming-crawling larva of 27 setigers that had been maintained without sediment had no branchial buds. Although west coast post-larval forms grew much more rapidly than their east coast counterparts, the appearance of branchiae was also age-dependent. Branchial buds appeared on the anterior segments of a 42-setiger specimen three weeks after metamorphosis.

As the organism develops the prostomium becomes more flaring anteriorly. A deep median longitudinal groove appears on the dorsal side, its sides thicken and the groove becomes a narrow slit. Although the time for its formation varies, the slit is usually complete by the 42-setiger stage. At about the latter stage the caruncle extends posteriorly to setiger 3, and rapidly beating short cilia can be seen on the dorsum lateral to the caruncle.

Small processes develop on the dorsal aspect of the two rounded lobes of the pygidium. Each process bears sensory cilia.

The growth rate of west coast post-larval stages was variable and was, at least in part, attributable to the type of substratum offered. Unwashed but previously air-dried sediment taken from the locality of adults in the estuary supported the best growth in the laboratory. Air-dried sediment mixed with open beach sand supported the poorest growth.

4. *Metamorphosis experiments*

During the summers of 1963, 1964 and 1965, several experiments were conducted to determine whether sediment of different sizes and from different sources, pieces of or entire snail shells, or sediment and shell together would hasten metamorphosis over that of larvae maintained in culture vessels. Data from a representative experiment are presented in Table II. In summary, larvae provided with sediment occasionally built tubes of sand within a few days. Usually these tubes were only temporary, for a larva would leave its tube, swim again, then settle and construct another tube. Larvae that settled in sediment seldom lived for more than a week after metamorphosing. On the other hand, those kept without sediment delayed metamorphosis, but once metamorphosis did occur, the young adults usually survived for a month or more. One larva, 62 days after its release from the egg mass, had attained 27 setigers in the absence of a substratum and still had not metamorphosed.

Recently, Meadows (1964) has shown that sediment that has either been washed with distilled water or air-dried becomes unattractive to two species of the

TABLE II
Metamorphosis of Boccardia hamata larvae on different substrates

Vessel	Treatment	Observations											
		8-5	8-7	8-11	8-15	8-17	8-19	8-23	8-30	9-6	9-11	9-13	9-18
4 larvae each	7-31-63												
A	Sed. + shell	4s + tubes	3s	1 in Sed. 2s	2s	1s	1s	0	0	0	0	0	0
B	Sed.	4s + tubes	4s	4s	4s	1s 1 in Sed.	0	0	0	0	0	0	0
C	Shell	4s	4s	2s	2s	2s	1s	1s	1m	1m	1m	1m	1m
D	—	4s	4s	4s	4s	4s	4s	4s	4s	3s	2s	2m	1m

Sed. = sediment; s = swimming larvae; m = metamorphosed larvae.

amphipod, *Corophium*. Since all sediment used in the above east coast experiments during 1963 and 1964 had been both washed in distilled water and air-dried, metamorphosis experiments were repeated during the summer of 1965 using untreated surface sediments (fine sand rich in detritus) from subtidal areas of the Mystic River. Settlement and metamorphosis were equally poor in these experiments as those with treated sediment.

An untreated *L. heros* shell that had previously contained a hermit crab was placed in a fingerbowl with filtered sea water and 10 late-stage *B. hamata* added. When examined after 7 days, two larvae had metamorphosed successfully on the shell's exterior and all but one pelagic larva had disappeared. Each metamorphosed larva had constructed a tube of silt-sized particles in a crevice, one in a growth line and one in a suture. When the tubes, which protruded from fresh excavations in the shell, were carefully dissected away, the excavations were already large enough to conceal the entire worm. On the 18th day of the experiment the shell was cracked open and the fragments examined. The two tongue-shaped burrows were ap-

proximately 0.5 mm. deep. No other *B. hamata* was found; however, one adult *Harmothoe imbricata* had been living inside the shell and may have eaten some of the settling larvae. It should be mentioned here that *H. imbricata* has been reared from trochophore to adulthood, the post-larvae thriving on a diet of polychaete larvae and copepods (Dean, unpublished).

Further studies on larval behavior and relationship to substrate are in progress and will be published later.

DISCUSSION

Pelagic larvae of *Boccardia hamata* are most easily distinguished from other polychaete larvae in the plankton on the basis of pigment pattern and body shape. Reference to the morphological details given here can serve to confirm the identification. When examining a plankton sample from the east coast under a dissecting microscope, larvae of *Polydora ciliata* and *P. ligni* are the ones most likely to be confused with *B. hamata*. Larvae of both *Polydora* species are generally more slender than those of *B. hamata*, but overlap in size and shape has been observed occasionally. Although the dorsal pigment pattern of the three species is similar, at least under low magnification, *B. hamata* larvae are readily separated from the *Polydora* species by the pigmentation of the lateral lips. On *B. hamata* the bars of dense black pigment are longitudinal while those on these two species of *Polydora* are transverse.

On the west coast, *B. hamata* larvae are most easily confused with larvae of *B. columbiana*, *B. proboscidea*, *B. tricuspa* and *Pseudopolydora kempi*. The three *Boccardia* species differ in having a single dorsal row of chromatophores. *B. columbiana* and *B. proboscidea* have bushy-topped modified setae in setiger 5, while *B. tricuspa* has modified setae with three cusps. *Pseudopolydora kempi* larvae have a dorsal pigment pattern similar to *B. hamata*, with medial and lateral rows of chromatophores. But *Ps. kempi* has no ventral pigment and the dorsal medial chromatophores are heavy and not composed of small circles of black pigment. Further, its fifth setiger has fully developed parapodial lobes.

Hartman (1941) has figured the larvae of *B. proboscidea* and Rioja (1939) has illustrated *B. tricuspa* larvae. *Pseudopolydora kempi* and *B. columbiana* larval development and supplementary data on *B. proboscidea* will be reported later by Dr. Keith H. Woodwick.

B. hamata larvae are planktotrophic once they are released from the egg sac. In plankton samples they attempted to ingest almost any object in their path. In laboratory culture they ingested liver powder so readily that their mid-sections became swollen, making their fusiform shape even more pronounced. Plump larvae as well as the more slender specimens so easily confused with *Polydora* were observed in plankton samples.

Although the 6-setiger stage is considered to be the first pelagic stage, larval stages as early as trochophores were removed from the egg string and appeared to develop normally. Specimens of *B. hamata* larvae younger than 6-setiger larvae were not recorded from the plankton during more than two years of study.

Hannerz (1956) found that in most spionid species the first segment to bear branchiae in the larva corresponds to the most anterior setiger bearing branchiae in the adult. He noted exceptions that occur in *Spio*, *Microspio* and *Pygospio*.

In the former two genera, branchiae appear first on the segment corresponding to the second branchial segment of the adult while in the latter, branchiae are lacking during the entire pelagic life and the first part of benthic life. With respect to the appearance of branchiae, *Boccardia hamata* occupies an intermediate position between *Pygospio* on one hand, and *Spio* and *Microspio* on the other. On adult *B. hamata* branchiae occur on setigers 2, 3, 6, 7, etc., while on its pelagic larvae neither branchiae nor branchial *anlage* are observed anterior to setiger 7. Branchial *anlage* appear on setigers 2, 3 and 6 approximately three weeks after metamorphosis has been completed. The appearance of anterior branchiae is dependent on age past metamorphosis regardless of the size of the young worm.

During the course of these investigations, several differences between east and west coast populations of larvae and adults have become apparent. While the pelagic larvae from both coasts are nearly identical morphologically, differences exist in behavior during the periods of larval settlement and metamorphosis (Table III). Larvae from west coast populations settle and metamorphose readily on a variety of substrates while those from the east coast seem to be much more

TABLE III

Major differences between B. hamata populations on the east and west coasts of North America

East Coast	West Coast
Absence of transverse band of dark pigment on setiger 2 of larvae	Band present
Larval metamorphosis difficult to induce in the laboratory (apparent high substrate-specificity)	Larvae metamorphose readily on a variety of substrates in the laboratory
Metamorphosis can be delayed > 2 mo.; pelagic larvae up to 27 setigers obtained	Metamorphosis rapid; no pelagic larvae > 19 setigers; settle and form mucus tubes
Adults usually found in burrows in shells	Adults in a variety of substrates, algal holdfasts, and occasionally shells

selective in choosing a substrate and can delay metamorphosis for extended periods. These behavioral differences are probably associated with habitat differences of the adults on the east and west coasts. Despite numerous benthic surveys by many workers on the Atlantic and Gulf coasts, there have been only a few records of this species and until now it has only been reported from galleries of shells (Webster, 1879; Hartman, 1951; Rioja, 1960). In the Pacific, on the other hand, it is more commonly found in tubes of mud or fine sand in shallow water (Berkeley, 1927; Okuda, 1937; Monro, 1938; Hartman, 1961; Blake, 1966). Certainly the survival of the east coast shell-associated forms would be enhanced by larvae with a high degree of substrate selectivity and ability to delay metamorphosis.

Nothing is known about larval development and behavior of *B. hamata* populations from the Gulf of Mexico. Since many temperate Atlantic species had continuous distributions across northern Florida into the Gulf of Mexico during high sea levels in the Pleistocene (Hedgpeth, 1953), it is likely that larval development and behavior of Gulf coast populations are very similar to, if not identical with those of east coast populations.

SUMMARY

1. Larval development of the spionid polychaete, *Boccardia hamata*, is described from specimens followed from eggs and plankton isolates to young adult stages. Trochophore, 4-, 12-, 13- and 19-setiger stages are illustrated.

2. Eggs are deposited in an egg string within the *Boccardia* burrow. Development within the string proceeds to the 6-setiger stage at which stage the larvae are released to the plankton. Pelagic larvae grow to the 16- to 19-setiger stage before settling and metamorphosing. Length of pelagic life is estimated to be about three weeks.

3. Larval development of this species on both east and west coasts is identical except for slight variations in pigmentation and ventral ciliation on the third setiger. The most important difference between the larvae is in larval behavior at the time of metamorphosis. West coast larvae metamorphose readily on a variety of substrata and are unable to delay metamorphosis beyond the 19-setiger stage. East coast larvae are much more selective in choosing a substratum and can delay metamorphosis for more than two months. It is suggested that these behavioral differences reflect habitat differences of the adults on the two coasts.

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